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EVIDENCE OF ASSORTIVE MATING IN A NUDIBRANCH

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In man there is found, according to Pearson and others, a slight but appreciable degree of positive correlation between the members of mating pairs as regards their stature and certain other characters. For *Paramecium* a similar, but higher, correlation was proved by Pearl (1907) to exist between the lengths of members of conjugating pairs. Jennings (1911) substantiated Pearl's discovery that in *Paramecium* large individuals are usually found mated with large, small individuals with small, and made more certain the conclusion that this correlation (homogamy) is due to real assortive mating, as Pearl had previously maintained.

This matter of assortive mating, which may have various important implications for evolution, appears not to have been studied in animals other than *Paramecium* and man. With reference to characters concerning the size of the organism, at least, it should, of course, be possible for assortive mating to take place only when there is available some physical basis for the required process of selection. Hence, although echinoderms and some other marine animals appear to congregate at their times of breeding, and may even be conspicuously disposed in pairs (Orton), it is not to be expected that invertebrates practicing external fertilization would, in general, yield any evidence of assortive mating. Among gastropods, however, the case is different, and notably so with nudibranchs. In the latter animals, which are hermaphroditic, a true copulation of two individuals seems a prerequisite for fertilization of the eggs. In some nudibranchs the male and female genital openings, two or three in number, situated on the right side of the body, are separated by a considerable distance, and the behavior of the animals in copulation shows that it is necessary for the 'male' and 'female' openings of one individual to be brought simultaneously into close relation with the appropriate openings of another (e.g., in *Cenia*, as described by Pelseneer, 1899).

Other nudibranchs, such as chromodorids, have the reproductive openings concentrated upon a single small papilla; but, in some cases, at least, their behavior during the maneuvers preliminary to actual copulation strongly suggests that here also there is a rather well-defined, though not absolute, mechanical necessity for equality in the sizes of

the individuals forming a successful mating pair. Reciprocal fertilization may be presumed to occur in most of these cases, and is certainly carried out in some instances.

The observation of mating pairs of *Chromodoris zebra* repeatedly suggested that under natural conditions this species forms copulating pairs of which the individual components closely correspond with each other in general size. Sexually mature specimens of this species range in length from 4 to 18 cm. Differences in the relative sizes of the various individuals are readily detected by the eye, while other dimensions of the animals may be subjected to measurement in the living condition.

One hundred and forty-eight pairs of copulating *C. zebra* were obtained in the field. The total length (anterior edge of the mantle to posterior termination of the foot) was determined for each specimen, according to a method² giving results sufficiently reproducible for the purposes of statistical treatment. As a check upon this measurement certain other dimensions were ascertained, including the weight and the volume. Each of the methods of evaluating size yields the same qualitative result. Therefore the estimations of total length according to the procedure employed may be relied upon as a criterion of assortive mating with respect to size. In figures 1 and 2, summarizing the observations upon mating pairs, total length measurements are used.

Figure 1 is a regression plot showing the correlation between the lengths of individuals and the average lengths of their mates, as found under natural circumstances. If the correlation were perfect, the observed points would lie upon line "(1)"; if no correlation were to be detected the regression line "(2)" would coincide with $m-m'$; actually the degree of correlation between the lengths of individuals composing copulating pairs is of about the same magnitude as that found in cultures of *Paramecium* containing a mixture of pure lines.

Laboratory experiments were carried out with over 400 specimens, embracing about 200 individuals originally obtained in pairs, and an approximately equal number of "single" nudibranchs. About 50 specimens, ranging in length from 4 or 6 to 16 or 18 cm., were placed in each of a number of 9-gallon aquaria supplied with running water. After two days the mating pairs noted in each aquarium were removed, and measured. Data were in this way obtained from 119 pairs, which had come together under such purposely contrived circumstances that true random mating might easily take place, since so many individuals were crowded together in a small space; while if assortive mating is in any degree a real condition of copulation it should still make its influ-

ence sufficiently evident. Measurements of these pairs are plotted in figure 2. The correlation between the members of mating pairs is in fact better than in the previous case (fig. 1); reasons for this will be discussed in a subsequent paper.

A study of the behavior of *Chromodoris* supports the view that there is exercised an active selection of mating partners. As a rule, two animals greatly differing in size do not successfully copulate. This has

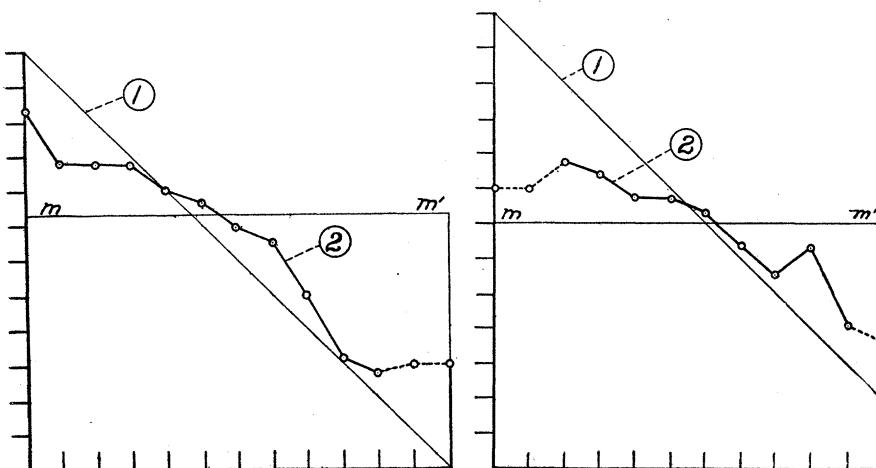


Fig. 1

Fig. 2

FIG. 1.—ILLUSTRATING THE CORRELATION IN SIZE BETWEEN THE MEMBERS OF 148 PAIRS OF *CHROMODORIS ZEBRA* COLLECTED IN THE FIELD

The thin continuous line (1) gives the lengths (as ordinates) for the different classes of individuals in order of decreasing size. The heavy line (2) gives the average lengths of the mates of the individuals of these classes. The unit is 1 cm; $m - m'$ is the mean for all.

FIG. 2.—ILLUSTRATING THE CORRELATION IN SIZE BETWEEN THE MEMBERS OF 119 PAIRS OBTAINED IN LABORATORY EXPERIMENTS

The thin continuous line (1) gives the lengths (as ordinates) for the different classes of individuals in order of decreasing size. The heavy line (2) gives the average lengths of the mates of these classes. The unit is 1 cm; $m - m'$ is the mean for all.

been verified by experiments in which the size of some individuals has been artificially reduced through starvation. The physical basis of assortive mating in *Chromodoris* is probably found in the relative attitudes assumed by the conjugants and in reactions to tactile (and chemical?) stimuli which determine these attitudes.

Two suggestions may be made regarding the possible significance of

assortive mating in *Chromodoris*. If the population is composed of a mixture of pure lines, then one effect of this type of copulation may well be, as in *Paramecium* (Jennings), the prevention of interlinear crossing. Certain generally accepted ideas regarding the life history of nudibranchs may tend to favor this view. The evidence for the presence of pure lines in the *Chromodoris* stock is, however, entirely inferential. It would, indeed, be almost impossible to obtain good evidence upon this point, unless, possibly, through a study of the rate of segmentation of the eggs; but the eggs of *C. zebra* are not well adapted for this work, and it is very doubtful if such evidence could be made conclusive.

Another, and, I believe, at present better founded, suggestion concerning the effect of assortive mating is based upon the fact that the size of the egg-masses, and the number of eggs in each ribbon, as well, probably, as the number of egg masses deposited by each animal during a single season, increase directly with the size of the individual. On grounds of physiological economy—remembering that mutual fertilization is involved, and remembering also that each animal deposits a number of egg-masses at each spawning season—it may be argued that the mating of large individuals is an influence tending to increase the number of larvae beyond that which would result from random pairing. In some other nudibranchs assortive mating, if it occurs, may have a different, or an additional, significance.

Summary.—Mating pairs of the nudibranch *Chromodoris zebra* are found to exhibit a rather high degree of correlation between the sizes of the two members. This is due to assortive mating, which may constitute an important influence tending to increase the numbers of larvae.

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² It was necessary to remove the animals from the water and place them, dorsal surface downward, upon a glass plate.

CORAL REEFS OF TUTUILA, WITH REFERENCE TO THE MURRAY AGASSIZ SOLUTION THEORY

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Tutuila, Samoa, is a purely volcanic island without elevated coral reefs or limestones. It is surrounded by a recent fringing reef which forms a mere veneer over the modern off-shore marine platform, and extends a short distance seaward, its precipitous outer edge being from